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Physiologic Specialization in Puccinia graminis avenae Erikss. and Henn.

Dixon L. Bailey
Division of Plant Pathology and Botany

UNIVERSITY FARM, ST. PAUL

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CONTENTS

PHYSIOLOGIC SPECIALIZATION IN PUCCINIA GRAMINIS AVENAE ERIKSS. AND HENN.[1]

DIXON L. BAILEY

INTRODUCTION

The over-shadowing importance of the wheat stem rust problem, together with the failure for a long time to demonstrate the existence of physiologic forms of *Puccinia graminis avenae* Erikss. and Henn. on oats, resulted to some extent in the neglect of the oat rust problem. The apparently ever-increasing economic importance of stem rust of oats, together with the demonstration of physiologic specialization in *P. graminis avenae* Erikss, and Henn. by Stakman, Levine, and Bailey (33) in 1923, has given added interest and a new significance to the problem, and has been largely responsible for the present investigation.[2]

HISTORICAL SUMMARY

It is questionable whether any other single event in the history of plant pathology has had so far-reaching an influence on the development of cereal pathology as the demonstration of physiologic specialization in *Puccinia graminis* Pers. by Eriksson (4)[3] in 1894. Much intensive work has been done on the subject since that time, with the result that our knowledge of the phenomenon has been increased to such an extent that today the significance of physiologic specialization is appreciated everywhere by those engaged in cereal rust investigations. This physiologic specialization is of the utmost importance, not only to a proper understanding of the parasitic behavior of rust fungi, but to the effective control of their ravages, as well.

A detailed review of the general field of physiologic specialization has been made by Reed (26), and a careful review of specialization in the cereal rusts by Stakman (28), Newton (23), and others. Therefore it seems unnecessary to do more here than merely to outline the significant advances which have led to our knowledge of specialization in cereal rusts.

[1] This investigation was a continuation of work done while the author was a member of the staff of the Office of Cereal Investigations, and of the Minnesota Agricultural Experiment Station.

This paper was submitted to the Faculty of the Graduate School of the University of Minnesota in partial fulfillment of the requirements for the Degree of Doctor of Philosophy, June, 1924.

[2] The writer wishes to express his appreciation of much help received from Dr. E. C. Stakman and Dr. M. N. Levine; as well as of the kindness of Mr. T. R. Stanton, Cereal Investigations, Bureau of Plant Industry, Washington, D. C.; and the Agronomy Department, University of Minnesota, in supplying seed of oat varieties. Dr. Alfred Savage, of Manitoba Agricultural College, also rendered much assistance in the preparation of the plates.

[3] Reference is made by number to "Literature cited," page 32.

For almost a century after it was described by Persoon, the stem rust organism, *Puccinia graminis,* was regarded as a single species capable of attacking all the common cereals and grasses. But in 1894 Eriksson (4), showed definitely that this single species comprised several distinct, physiologically specialized races, each limited in infection capabilities to a definite and distinctive group of cereals and grasses. Six such races, or varieties, of *P. graminis* have been found to occur on the North American continent, and are designated as follows: *Puccinia graminis tritici; P. graminis secalis; P. graminis avenae; P. graminis phleipratensis; P. graminis agrostis;* and *P. graminis poae.* They have come to be known as the six major physiologic forms, or recently as varieties of *P. graminis.*

Since 1894 many investigators have studied the physiologic specialization of *P. graminis.* In Europe, Eriksson (4, 5), Eriksson and Henning (6), Ward (40, 41), Jaczewski (16), and Vavilov (39) have been outstanding; while in America, Hitchcock and Carleton (12), Carleton (2, 3), Freeman and Johnson (9), Johnson (17), Stakman (28) Stakman and Piemeisel (37), Stakman and Levine (32), Fraser (7), Newton (23), Levine (19), and others have contributed much to our knowledge of the subject.

Much of the earlier work dealt largely with the host range and constancy of the several physiologic forms. In 1916, however, Stakman and Piemeisel (36) showed that further specialization existed within *P. graminis tritici.* Subsequent research on the specialization of *P. graminis* has dealt in the main with these component physiologic forms. The most extensive work has been done by Stakman and Levine and their co-workers (18-21, 28-38), at the University of Minnesota, in co-operation with the United States Department of Agriculture. These investigators have demonstrated (32) the existence of at least 37 physiologic forms of *P. graminis tritici,* distinguished by their action on twelve wheat varieties. A limited number of forms of *P. graminis secalis* and *P. graminis avenae* on varieties of rye and oats have also been demonstrated (21, 33).

The physiologic specialization of several other species of rust fungi also has been investigated, and has been found to be of wide occurrence. It was demonstrated in *P. coronata avenae* Cda. by Hoerner (13, 14) in 1919; in *P. triticina* Erikss., in 1921 by Mains and Jackson (22); and in *P. glumarum* previously by Eriksson (4) and in 1923 by Hungerford and Owens (15).

The extent of the investigations on physiologic specialization is sufficient evidence of the importance of the subject. Indeed, as the development of resistant varieties is one of the most promising methods of combating cereal rusts in general, it is evident that, in each particular case, the solution of a rust problem requires a thoro investigation of the physiologic specialization of the causal organism. Only in this way can resistant varieties be chosen or developed with any assurance that their resistance will be adequate in all localities and at all times.

OBJECTS OF PRESENT INVESTIGATION

The present investigation of physiologic specialization in *P. graminis avenae* and its relation to the oat stem rust problem in general, was practically a continuation of the investigations begun by Stakman, Levine, and Bailey and reported by them (33) in 1923. The apparently increasing destructiveness of stem rust of oats in the last few years made it desirable to know more of the nature and occurrence of the forms of *P. graminis avenae,* so that resistant varieties of oats could be developed.

Accordingly, extensive collections of stem rust on oats have been obtained and cultivated in the greenhouse. The reaction of a large number of varieties to these cultures has been determined. The physiologic forms isolated on the basis of their effect on the differential varieties have been carefully studied and are reported on here.

METHODS AND MATERIALS

Differential hosts.—The selection of differential hosts was difficult. More than a hundred varieties of oats, belonging to six species of the genus *Avena,* were tested as differentials; and from this number only six differential hosts were obtained. Five of these, namely: Richland (C.I. 787) and the pure line isolations from Monarch Selection (C.I. 1879), Joanette (C.I. 1880), and the Heigira Rustproof (C.I. 1001), and Strain 703, belong to *Avena sativa,* while the sixth, White Tartar (C.I. 551) is a variety of *Avena orientalis.* While all six of these lines are differential, it appears from results to date that some of them are identical in resistance and that they really represent only three groups of differentials, as follows: (1) Joanette and Strain 703; (2) Richland, Heigira Rustproof, and Monarch Selection; and (3) White Tartar.

The first of the pure lines to be obtained, which is designated throughout this work as "Strain 703," apparently originated from the Monarch Selection of Etheridge. Indeed, it was thought to be identical with Monarch Selection until the original supply of seed was practically exhausted and additional lots of seed were obtained from different sources. In general, the plants grown from these lots of seed were entirely susceptible. Resistant plants of the original sample were therefore selected as the basis of a pure-line differential host. This line has been designated simply as Strain 703, after the nursery row number under which it originally came to us.

The variety Joanette (C.I. 1880) also was found to contain pure lines of differential value, altho, like Strain 703, the stock material was not genetically pure in its resistance, and the differential line had to be developed from selected plants of known resistance. Several samples of Joanette were obtained which were wholly without resistance, and the origin of the differential line is unknown. In its reaction, the selected line, henceforth designated as Joanette Strain, is apparently identical with Strain 703.

An occasional plant in a sample of Monarch Selection (C.I. 1879) received from the Office of Cereal Investigations, United States Department of Agriculture, was found to react differently to different cultures of *P. graminis avenae*. A few of these plants, chosen on the basis of their resistance, were increased to serve as a possible differential line. The name "Monarch Strain" was chosen for this line to distinguish it from the Monarch Selection of Etheridge, which was used as a differential variety in previous work (33). The name "Monarch Strain," however, is more indicative of its origin than of its nature, as the bulk of Monarch Selection seems to be altogether without resistance. Monarch Strain differs very little in its reaction from Richland and Heigira Rustproof and may for the present be included with them as one differential group.

As about five per cent of the plants of Heigira Rustproof (C.I. 1001) were without resistance, it was necessary to select a pure line differential of this variety also, to be known from now on as "Heigira Strain." This strain, however, was not different in its reaction to the various forms of *P. graminis avenae* from Monarch Strain and Richland, the three constituting a single differential group.

Lines of satisfactory purity of the remaining differentials, Richland (C.I. 787, Iowa 105) and White Tartar (White Russian) (C.I. 551, Minn. 339), were available without selection.

Progress of the work was much retarded by the necessity of developing pure lines of the various differential hosts. Even yet the amount of available seed of Monarch Strain and of Strain 703 is so limited that it often has not been possible to use nearly as many plants as was desired.

CLASSES OF HOST REACTION AND INFECTION TYPES

The classes and sub-classes of host reaction as well as the infection types indicated by Stakman, Levine, and Bailey (33) have been followed. These are as follows:

Classes of Host Reaction		Types of Rust Infection
Practically immune	0.	No uredinia developed, but sharply defined hypersensitive flecks present.
Extremely resistant	1.	Infection very light; uredinia minute, scattered, and surrounded by sharply defined necrotic areas.
Moderately resistant	2.	Infection light; uredinia usually small and scattered, hypersensitive areas varying from sharply defined necrosis to pronounced chlorosis.
Moderately susceptible	3.	Infection moderate; uredinia mid-sized with a tendency to coalesce; true hypersensitiveness absent, but more or less well marked chlorosis present.
Completely susceptible	4.	Infection normal and heavy; uredinia large, numerous, and confluent; hypersensitiveness absent, but chlorosis may be present.
Indeterminate	X.	Uredinia very variable, apparently including all types of infection, often on the same leaf blade; no mechanical separation of the types seems possible, and the infection in general is ill-defined and heterogeneous.

These types of infection are illustrated in Plate 1, and a more detailed description of their characteristics and variability is included in the subsequent discussion of the individual forms.

IDENTIFICATION OF PHYSIOLOGIC FORMS

An analytical key to the physiologic forms of *P. graminis avenae,* which serves to identify the individual forms by the reaction of the above mentioned differential hosts, is given in Table I.

TABLE I

Analytical Key for Identification of Physiologic Forms of *P. graminis avenae*

Infection homogeneous on all differential hosts
- White Tartar resistant
  - Joanette Strain resistant .... Form 1
  - Joanette Strain susceptible .... Form 2
- White Tartar susceptible
  - Richland resistant .... Form 3
  - Richland susceptible .... Form 4

Infection heterogeneous on some differential hosts
- Joanette Strain indeterminate .... Form 5

EXPERIMENTAL RESULTS

Classification of physiologic forms.—Five physiologic forms of *P. graminis avenae* have been isolated. A summary of the infection characteristics of these forms on six differential hosts and on one control variety is presented in Table II. A discussion of the characteristics of each form follows:

TABLE II

VARIATIONS AND CONSTANTS IN REACTION OF DIFFERENTIAL HOSTS OF AVENA SPP. TO PHYSIOLOGIC FORMS OF *P. graminis avenae*

Physiologic forms	Differential hosts with ranges and means of infection						Control host	
	White Tartar		Joanette Strain and Strain 703		Richland, Monarch and Heigira Strains		Victory	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean
1	2— to 3—cn.	3—	0; to 1++	1	2 to 2++	2	4— to 4++	4
2	2— to 3—cn.	3—	4— to 4+	4	1— to 2++	2	4— to 4++	4
3	3 to 4+	4—	0; to 1	1—	2— to 2++	2	4— to 4++	4
4	4— to 4++	4	0; to 1	1—	4— to 4++	4	4— to 4++	4+
5	2— to 3—cn.	3—	X— to X+	X	1— to 2++	2	4— to 4++	4

Explanation of symbols: Plus and minus signs indicate a slightly greater or less amount of rust than the nearest figure representing the infection type. The semicolon indicates the presence of flecks. —cn. indicates that hypersentiveness ranging from chlorosis to necrosis typically accompanies the infection.

NATURE OF FORMS ISOLATED

Form 1.—This form is singularly lacking in virulence on the differential hosts used. It is incapable of infecting normally any of the differentials except Victory, which, it will be remembered, is equally susceptible to all the physiologic forms and therefore is not really differential. The reaction of the various differential hosts to Form 1 is illustrated in Plate 2.

Strain 703 is extremely resistant to Form 1. Its reaction varies from the production of only sharply necrotic flecks without any uredinia to the production of fairly abundant, small uredinia, each surrounded by a very definite necrotic area. That is, the type of infection varies from 0, with flecks, to 1++. The degree of infection seems to be very largely a reflection of existing environmental conditions. As the light intensity is reduced or the temperature lowered, the infection becomes progressively weaker, until necrotic flecks are the only evidence that infection has taken place. Even under optimum environmental conditions infection is decidedly limited, and belongs in type 1, altho there is a slight increase in the size of the uredinia.

The reaction of Joanette Strain to Form 1 is practically identical with that of Strain 703. At times the range of infection on Joanette seemed somewhat more limited, with the maximum 1 rather than 1+. The difference, however, was not at all striking.

Richland and Heigira Strain are infected to about the same degree by Form 1. The infection is of type 2, with the extreme variations approaching type 1 and, rarely, type 3. Usually, however, in the weak infections the uredinia are too large for type 1, while in the most vigorous infections hypersensitiveness is too marked for type 3. There is a distinct tendency in Richland, especially when environmental conditions are not optimum, for infected tips to parch and die before uredinia are developed, or about the time they begin to break through the epidermis.

A type 2 infection is characteristic of Monarch Strain when infected by Form 1. The pustules are usually smaller than the average in type 3 infections, but only a moderate chlorosis is associated with the uredinia.

In the infection of White Tartar by Form 1, there is considerable variation in the size of the uredinia. Pustules varying from 3— to 3= are commonly met with. The infection is always accompanied by some chlorosis altho in this respect there is the greatest variation. Sometimes chlorosis is so slight as to be scarcely noticeable except on the upper surface of the leaf; at other times it is so pronounced as to merge almost into necrosis. The variation seems to be associated with the number of uredinia in the infected area as well as with environmental conditions, especially light intensity. Other factors may well be operating, but the reaction is still very imperfectly understood. The chlorosis, instead of delimiting the individual uredinia, is usually diffused.

Generally speaking, Form 1 infects the various differential hosts weakly, and is remarkably constant. One culture, collected in 1921, has been cultured for 40 urediniospore generations. At the end of that time it produced typical infection on all the differential hosts. The history of this particular culture is summed up in Table IV, as an example of the cultural characteristics of Form 1. In view of the limited infection capabilities of Form 1 in relation to the differential varieties, its wide distribution and comparative frequency of occurrence (see Table XIX) seemed difficult to explain. In order to obtain a better idea of its virulence, the reaction of a large number of standard oat varieties to Form 1 was determined. The results are given in Table III, where it will be seen that, even tho Form 1 is conspicuously lacking in virulence with respect to the differential hosts as compared with the other forms, it is nevertheless capable of infecting normally each of the 56 oat varieties tested. Its grass-host range, too (Table XVII), is not, so far as has been investigated, significantly more limited than that of the other forms. Consequently, it seems that Form 1 should be regarded as lacking in virulence only in relation to the three differential groups.

TABLE III

REACTION OF SPECIES AND VARIETIES OF AVENA TO *P. graminis avenae*, Form 1

Varietal name*	Classification	Plants inoculated	Plants infected†
Avena nuda	*Avena nuda*	12	10
A. strigosa	*A. strigosa*	10	10
A. brevis	*A. brevis*	10	10
A. sterilis nigra	*A. sterilis*	6	5
A. sterilis (selection)	do	10	10
Red Rustproof	do	11	9
Burt	do	9	9
King	do	8	8
Oklahoma 606	do	10	7
Winter Turf	*A. sativa*	8	7
Culbertson	do	12	12
Black Norway	do	14	14
Victor	do	10	9
Monarch	do	10	10
Black Mesdag	do	9	9
Black Diamond	do	12	12
Joanette	do	15	14
C.I. 620	do	14	13
North Finnish	do	14	14
Garkova 473	do	14	12
Garkova 691	do	12	10
Kherson	do	10	9
Kherson selection	do	10	10
60-Day	do	12	10
60-Day Selection	do	14	12
Early Champion	do	14	14
Awnless Probsteier	do	10	9
Japan Selection	do	15	11
Golden Drop	do	12	10
C.I. 603	do	14	12
Green Russian	do	14	14
Monarch Diamond	do	10	9
Canadian	do	10	10
Tobolsk	do	12	10
Early Dakota	do	14	14
Irish Victor	do	12	10
Danish Island	do	9	8
Early Gothland	do	14	12
Belyak	do	14	14
Silvermine	do	10	10
Scottish Chief	do	12	12
June	do	12	12
Swedish Select	do	13	11
Lincoln	do	12	12
Golden Rain	do	10	10
Banner	do	12	12
Ligowa	do	21	16
Garton 748	*A. orientalis*	10	10
Garton 84	do	10	10
Garton Gray	do	12	10
Black Tartarian	do	14	12
Golden Giant	do	14	14
Sparrowbill	do	12	12
Garton 585	do	12	12
Tartar King	do	12	10
Storm King	do	12	11

* The U. S. Department of Agriculture Cereal Investigation numbers are omitted, as they are given in Table XVII.

† Infection type 4 throughout, except first 3 species on which the rust produced a type 3 infection.

Form 2.—Form 2 is distinguished from Form 1 only by the reactions of Strain 703 and Joanette Strain. These differentials are completely susceptible instead of being resistant, as they are to Form 1. When these hosts are inoculated with Form 2, numerous large, vigorous uredinia develop, which commonly coalesce. As a rule there is no associated chlorosis, altho occasionally a slight amount is present, especially if the infection is very heavy. As this phenomenon is common in the majority of thoroly susceptible varieties, it seems not to have any particular significance here.

The other differentials—White Tartar, Monarch Strain, Heigira Strain and Richland—are all resistant to Form 2. Their various reactions to Form 2 apparently are identical with those to Form 1. The reaction of all the differential hosts to Form 2 is illustrated in Plate 3.

Form 2 was found to infect all the oat varieties which were tested with Form 1 (See Table III). All the varieties were so susceptible and the infections so uniform that it seems undesirable to record the details. The infection capabilities of one collection of Form 2 have remained unchanged through 29 urediniospore generations. A summarized cultural history of a collection of Form 2 is given in Table IV.

Form 3.—Form 3 is similar to Form 1, except for the reaction of White Tartar, which is susceptible to Form 3. Therefore with Form 3 we have the varieties Victory and White Tartar completely susceptible; while Joanette Strain and Strain 703 on the one hand, and Richland, Heigira Strain, and Monarch Strain on the other, are still very resistant. The last three hosts react to Form 3 in much the same way as to Forms 1 and 2, the reaction being some variation of type 2. Joanette Strain and Strain 703 are quite as resistant to Form 3 as to Form 1. The infection characteristics of Form 3 are illustrated in Plate 4.

Only two collections of Form 3 have been obtained, and neither of these was of American origin. One was collected by E. C. Stakman in Sweden (Upsala) and the other by G. F. Puttick in South Africa (Potchefstroom, Transvaal) (33). The cultural history of the South African collection is given in Table IV.

Form 4.—This is an exceedingly virulent form to which all the differential hosts except Joanette Strain and Strain 703, are completely susceptible. Even Heigira Strain, Richland, and Monarch Strain, resistant to all the other forms, are infected by Form 4 as heavily as is Victory, which is susceptible to all the forms.

Form 4 is represented by a single culture, collected by Stakman at Upsala, Sweden. Its cultural history is given in Table IV. The reaction of the various differential hosts to Form 4 is shown in Plate 5.

Form 5.—The most characteristic reaction of Form 5 is the heterogeneous type of infection which develops on Joanette Strain and

Strain 703 when infected by it. This type of infection is shown in Plate 1, F. It is characterized by the great variability both in pustule size and in degree of hypersensitiveness, which is found on even a single infected leaf. All types of infection from 1 to 4 are commonly found on the same leaf, with a hypersensitiveness which may vary from a faint chlorosis to a sharp necrosis also usually present. The different types of infection are not separable by the ordinary method of mechanical separation. Transfers from any particular type usually result in all the infection types from 1 to 4 occurring again in the subsequent infection. This seems to indicate that the form is not a mechanical mixture of several forms.

In order to ascertain whether Form 5 was a mixture of other forms, a monosporous culture was obtained. Single spores were picked up directly from a dry slide on a needle very slightly smeared with vaseline, a No. 2 eyepiece and low-power objective being used during the process. A single spore was transferred to a seedling and the inoculated plants were then incubated as usual. Scarcely more than one half of one per cent of the inoculated leaves became infected.

Only one such single-spore culture has yet been compared with the original strain. In this case, what seems to be a perfectly typical culture of Form 2 was isolated. Strain 703 and Joanette Strain have been completely susceptible to the single-spore strain for two urediniospore generations, while the original strain continues to produce the same heterogeneous infection on these varieties. Further trials are in progress. It is recognized that a single trial does not warrant drawing any general conclusions. The indication is, however, that Form 5 may be a mixture of Form 2 and another form from which it is separated only with very great difficulty. Even if this be the case there probably is a fifth form present, because the other four forms produce infection of either type 1 or type 4 on Joanette Strain and Strain 703, and this leaves the intermediate types which are present in the X reaction unaccounted for. The final clearing up of the problem must await more extended investigations.

The summarized history of a culture of Form 5 is given in Table IV and is illustrated in Plate 6.

TABLE IV

PARASITIC BEHAVIOR OF TYPICAL CULTURES OF FIVE PHYSIOLOGIC FORMS OF *P. graminis avenae*

Subject matter	Host reaction — Differential hosts: White Tartar	Joanette Strain and Strain 703	Richland, Monarch, and Heigira Strains	Control host: Victory
P. graminis avenae, Form 1 — Collected Aug. 12, 1921, on Victory oats at St. Paul, Minn.				
Number of trials....	12	11	9	26
Plants inoculated ...	150	105	113	315
Plants infected	146	96*	113	296
Range of infection...	2— to 3†	0; to 1++	2— to 2+	4 to 4+
P. graminis avenae, Form 2 — Collected Aug. 1, 1923, at Melfort, Sask.				
Number of trials....	1	4	6	8
Plants inoculated ...	17	66	74	89
Plants infected	16	58	70	83
Range of infection...	2— to 3†	4 to 4	2— to 2	4 to 4+
P. graminis avenae. Form 3 — Collected May 11, 1922, at Potchefstroom, South Africa				
Number of trials....	18	5	17	14
Plants inoculated ...	194	78	225	167
Plants infected	185	56	217	150
Range of infection...	3 to 4	0; to 1	2— to 2	4 to 4+
P. graminis avenae, Form 4 — Collected Sept. 14, 1922, at Upsala, Sweden				
Number of trials....	6	7	15	10
Plants inoculated ...	82	91	173	127
Plants infected	78	79	170	122
Range of infection...	4— to 4	1— to 1	4-- to 4	4 to 4+
P. graminis avenae, Form 5 — Cellected Aug. 8, 1913, at Morden, Man.				
Number of trials....	2	7	7	5
Plants inoculated ...	27	74	73	54
Plants infected	27	70	66	50
Range of infection...	2— to 3†	X to X+	2— to 2	4 to 4+

* There were also three heavily infected plants, probably due to accidental seed mixture.
† Hypersensitiveness—chlorosis to necrosis—regularly present.

MORPHOLOGICAL DIFFERENCES BETWEEN THE PHYSIOLOGIC FORMS

Levine (19) has shown recently that when the major physiologic forms or varieties of *Puccinia graminis* are developed under identical conditions, each variety is characterized by spore measurements differing significantly from those of other varieties. The morphological identity of minor physiologic forms has been studied heretofore only in an empirical way (31). Consequently, it seemed desirable to study statistically the spore measurements of the urediniospores of the physiologic forms of *P. graminis avenae* in order to determine whether they differ significantly in size. Such a study seemed particularly desirable, as the spores of *P. graminis avenae* have long been recognized as the most variable of any of the varieties of *P. graminis*.

Accordingly, 200 urediniospores of each of Forms 1, 3, 4, and 5 produced on congenial hosts under similar conditions, were measured by means of an ocular micrometer. From the measurements so obtained, the various biometric constants of spore length and spore width were calculated and compared. The results are given in Tables V to VIII inclusive. A study of the tables indicates that there are apparently appreciable and significant differences between the mean spore dimensions of the different forms. For instance, the urediniospores of Form 4 are significantly longer and wider than those of the other three forms. Likewise those of Form 3 seem longer but narrower than those of Forms 5 and 1. The suggestion of a correlation between spore length and virulence is interesting.

TABLE V

FREQUENCY DISTRIBUTION FOR LENGTHS OF 200 UREDINIOSPORES OF *P. graminis avenae* FORMS 1, 3, 4, AND 5, DEVELOPED UNDER IDENTICAL CONDITIONS

Physiologic form	Spore length (in microns) — Frequency classes																		Total population
	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	
1	1	0	1	2	33	13	11	32	62	22	2	4	12	5	0	0	0	0	200
3	3	1	2	6	27	6	17	22	43	19	3	14	14	18	3	1	0	1	200
4	0	0	0	0	9	1	5	15	63	24	2	25	22	22	7	3	0	2	200
5	0	2	1	1	55	21	13	29	45	10	1	13	7	2	0	0	0	0	200

TABLE VI

FREQUENCY DISTRIBUTION FOR WIDTHS OF UREDINIOSPORES OF *P. graminis avenae*, FORMS 1, 3, 4, AND 5, DEVELOPED UNDER IDENTICAL CONDITIONS

Physiologic form	Spore width (in microns) — Frequency classes										Total population
	13	14	15	16	17	18	19	20	21	22	
1	0	4	24	36	96	24	7	3	1	5	200
3	23	32	46	35	62	2	0	0	0	0	200
4	2	1	8	22	123	27	12	2	1	2	200
5	12	16	22	46	70	21	5	4	1	3	200

TABLE VII

CONSTANTS OF SPORE DIMENSIONS OF UREDINIOSPORES OF PHYSIOLOGIC FORMS OF *P. graminis avenae*, DEVELOPED UNDER IDENTICAL CONDITIONS

Physiologic form	Spore length (in microns)			Spore width (in microns)		
	Mean	Standard deviation	Coefficient of variability	Mean	Standard deviation	Coefficient of variability
1	29.41 ± 0.12	2.43 ± 0.08	8.2 ± 0.27	16.90 ± 0.07	1.30 ± 0.05	8.2 ± .27
3	30.03 ± 0.15	3.24 ± 0.11	10.7 ± 0.51	15.44 ± 0.07	1.39 ± .05	9.01 ± 0.42
4	31.50 ± 0.13	2.7 ± 0.09	8.6 ± 0.29	17.11 ± 0.05	1.13 ± .04	6.5 ± 0.22
5	28.63 ± 0.14	2.83 ± 0.09	9.6 ± 0.45	16.38 ± 0.08	1.69 ± .06	10.3 ± 0.48

TABLE VIII

SUMMARY OF DIFFERENCES BETWEEN THE MEANS AND COEFFICIENTS OF VARIABILITY OF UREDINIOSPORE DIMENSIONS OF PHYSIOLOGIC FORMS OF *P. graminis avenae* DEVELOPED UNDER IDENTICAL CONDITIONS

Physiologic forms compared	Arithmetical means				Coefficients of variability			
	Length		Width		Length		Width	
	Difference in means (in microns)	Difference divided by P.E.	Difference in means (in microns)	Difference divided by P.E.	Difference in means (in microns)	Difference divided by P.E.	Difference in means (in microns)	Difference divided by P.E.
P. graminis avenae 1 and 3....	0.62±0.19	3.26	1.46±0.09	16.22	2.5±0.58	4.31	0.8±0.50	1.60
do 4	2.09±0.18	11.61	0.21±0.07	3.00	0.4±0.39	1.02	1.7±0.34	5.00
do 5	0.78±0.18	4.33	0.52±0.10	5.20	1.4±0.52	2.69	2.1±0.44	4.77
P. graminis avenae 3 and 4....	1.47±0.19	7.73	1.67±0.07	20.87	2.1±0.58	3.62	2.5±0.47	5.32
do 5	1.40±0.20	7.00	0.94±0.10	9.40	1.1±0.68	1.47	1.3±0.63	2.06
P. graminis avenae 4 and 5....	2.87±0.23	12.48	0.73±0.09	8.11	1.0±0.53	1.89	3.8±0.48	7.92

TABLE IX

FREQUENCY DISTRIBUTIONS OF SPORE LENGTHS OF UREDINIOSPORES OF A SINGLE-SPORE CULTURE AND OF A BULK CULTURE OF *P. graminis avenae*, FORM 5

Type of culture	Frequency classes for spore length (in microns)												Total population
	24	25	26	27	28	29	30	31	32	33	34	35	
Single-spore culture	3	3	14	6	9	11	31	7	1	6	2	7	100
Bulk culture	0	2	18	3	8	12	34	8	3	6	1	5	100

TABLE X

FREQUENCY DISTRIBUTIONS OF SPORE WIDTH OF UREDINIOSPORES OF A SINGLE-SPORE CULTURE AND OF A BULK CULTURE OF *P. graminis avenae*, Form 5

Type of culture	Frequency classes for spore width (in microns)										Total population
	13	14	15	16	17	18	19	20	21	22	
Single-spore culture ..	2	3	13	15	48	11	6	0	2	0	100
Bulk culture	1	3	13	16	49	11	4	2	0	1	100

TABLE XI

COMPARISON OF CONSTANTS OF SPORE DIMENSIONS OF UREDINIOSPORES OF A BULK AND A MONOSPOROUS CULTURE OF *P. graminis avenae*, Form 5

Type of culture	Constants of spore length			Constants of spore width		
	Mean	Standard deviation	Coefficient of variability	Mean	Standard deviation	Coefficient of variability
Monosporous ...	29.34 ± 0.16	2.45 ± 0.12	8.4 ± 0.40	16.63 ± 0.12	1.34 ± 0.07	8.1 ± 0.39
Bulk	29.44 ± 0.16	2.4 ± 0.11	8.1 ± 0.38	16.75 ± 0.12	1.32 ± 0.06	7.8 ± 0.37

A comparison of the coefficients of variability for spore lengths indicates that the urediniospores of Form 3 are somewhat more variable in length than those of Forms 1 and 4. These results suggest that the marked variability of spore size in *P. graminis avenae* is an inherent character and is not due to the mixing of the spores of a number of physiologic forms differing greatly in spore size. This conclusion was substantiated still further by the results of a comparison of spore size and variability of a single-spore culture as compared with a bulk culture of Form 5. In this case one hundred spores of each culture were measured. As will be seen by a study of Tables IX, X, XI and XII, there was no significant difference between the two in either spore length, spore width, or variability.

TABLE XII

DIFFERENCES IN THE MEANS AND COEFFICIENTS OF VARIABILITY OF UREDINIOSPORE DIMENSIONS OF A SINGLE-SPORE CULTURE AND OF A BULK CULTURE OF *P. graminis avenae*—Form 5

Cultures compared	Arithmetical means				Coefficients of variability			
	Length		Width		Length		Width	
	Difference in means (in microns)	Difference divided by P.E.	Difference in means (in microns)	Difference divided by P.E.	Difference in means (in microns)	Difference divided by P.E.	Difference in means (in microns)	Difference divided by P.E.
Monosporous and bulk	0.10±.23	0.43	0.12±.17	0.71	0.3±.55	0.55	0.3±.54	0.56

TABLE XIII

FREQUENCY DISTRIBUTION FOR LENGTHS OF UREDINIOSPORES OF PHYSIOLOGIC FORMS OF *P. graminis avenae* DEVELOPED UNDER VARIOUS ENVIRONMENTAL CONDITIONS AND ON DIFFERENT HOST PLANTS

Physiolgoic forms	Conditions	Frequency classes for spore length (in microns)																		Total population
		18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	
Form 1	Resistant host	0	0	1	1	17	2	17	21	82	16	6	21	15	1	0	0	0	0	200
	Susceptible host	0	0	0	0	4	0	15	13	63	29	22	34	15	3	0	2	0	0	200
Form 2	Optimum	0	0	0	0	9	0	12	15	68	16	12	29	31	3	1	4	0	0	200
	Reduced light	1	2	1	7	40	3	22	22	56	17	8	12	7	2	0	0	0	0	200
	Excessive humidity	0	0	0	0	0	0	2	4	41	20	20	41	49	10	2	4	0	7	200
	Deficient soil moisture	0	0	0	0	15	5	16	16	44	11	14	36	31	5	0	5	0	2	200

TABLE XIV

FREQUENCY DISTRIBUTION FOR WIDTHS OF UREDINIOSPORES OF PHYSIOLOGIC FORMS OF *P. graminis avenae* DEVELOPED UNDER VARIOUS ENVIRONMENTAL CONDITIONS AND ON DIFFERENT HOST PLANTS

Physiologic forms	Conditions	Frequency classes for spore width (in microns)												Total population
		11	12	13	14	15	16	17	18	19	20	21	22	
Form 1	Resistant host	0	0	0	0	8	17	72	44	21	21	7	10	200
	Susceptible host	0	0	29	28	52	48	38	5	0	0	0	0	200
Form 2	Optimum	0	0	43	29	46	36	43	3	0	0	0	0	200
	Reduced light	1	2	51	40	50	34	21	1	0	0	0	0	200
	Excessive humidity	0	0	10	22	34	42	66	15	5	2	2	2	200
	Deficient soil moisture	0	0	36	30	43	34	43	6	5	3	0	0	200

TABLE XV

INFLUENCE OF ENVIRONMENTAL CONDITIONS AND HOST PLANTS ON THE SIZE OF UREDINIOSPORES OF PHYSIOLOGIC FORMS OF *P. graminis avenae*

Physiologic form	Conditions	Constants for					
		Spore length			Spore width		
		Mean	Standard deviation	Coefficient of variability	Mean	Standard deviation	Coefficient of variability
Form 1	Congenial host	27.02±0.11	2.43±0.08	8.9 ±0.30	15.26±0.06	1.41±0.05	9.2±0.31
	Resistant host	26.08±0.10	2.13±0.07	8.2 ±0.27	17.97±0.05	1.64±0.05	9.1±0.31
Form 2	Optimum	27.12±0.11	2.3 ±0.08	8.5 ±0.28	15.08±0.07	1.45±0.05	9.6±0.32
	Reduced light	24.95±0.12	2.54±0.08	10.2 ±0.34	14.60±0.06	1.38±0.05	9.4±0.32
	Excessive humidity	28.64±0.11	2.2 ±0.07	7.6 ±0.23	16.70±0.08	1.69±0.06	10.4±0.35
	Deficient moisture	27.13±0.13	2.74±0.09	10.1 ±0.34	15.40±0.07	1.43±0.05	9.3±0.31

TABLE XVI

SUMMARY OF DIFFERENCES IN THE MEANS AND COEFFICIENTS OF VARIABILITY OF UREDINIOSPORES OF PHYSIOLOGIC FORMS OF *P. graminis avenae* DEVELOPED UNDER VARIOUS ENVIRONMENTAL CONDITIONS AND ON DIFFERENT HOST PLANTS

Physiologic form	Conditions compared	Arithmetical means				Coefficients of variability			
		Length		Width		Length		Width	
		Difference in means (in microns)	Difference divided by P.E.	Difference in means (in microns)	Difference divided by P.E.	Difference in means (in microns)	Difference divided by P.E.	Difference in means (in microns)	Difference divided by P.E.
Form 1	Congenial and resistant hosts..	0.94±.15	6.27	2.71±.08	33.88	0.7±.40	1.75	0.1±.44	0.23
Form 2	Optimum and reduced light...	2.17±.16	13.56	0.48±.09	5.33	1.7±.44	3.86	0.2±.45	0.44
	do ..... excess humidity...	1.52±.16	9.50	1.62±.10	16.20	0.9±.36	2.50	0.8±.47	1.70
	do ... deficient moisture...	0.01±.17	0.06	0.32±.10	3.20	1.6±.44	3.64	0.3±.45	0.67
	Reduced light and excess humidity...	3.69±.16	23.06	1.62±.09	18.00	2.6±.41	6.34	1.0±.47	2.13
	do ... deficient moisture...	2.18±.18	12.11	0.80±.09	8.89	0.1±.48	0.02	0.1±.45	0.22
	Excess humidity and deficient moisture	1.51±.17	8.88	1.30±.10	1.30	2.5±.41	6.10	1.1±.47	2.34

In view of the fact that environmental conditions have been shown to influence spore size in *P. graminis* (31, 19), it seemed advisable to compare the above differences in spore size of the various forms with the differences induced in a single form by altered environmental conditions. Accordingly, the influence of an uncongenial host, of decreased light intensity, of excessive drouth, and of high humidity on the size of urediniospores of Form 2, was investigated. In each case, 200 spores were measured as before and the biometric constants of spore length and spore width were calculated. The results are presented in Tables XIII, XIV, XV, and XVI.

It will be noticed that altered environmental conditions resulted in changes in spore size as great as or even greater than the differences that existed between the spores of the different forms produced under identical conditions. Thus, reduced light intensity has a marked effect in reducing spore size and increasing variability. Excessive humidity, on the contrary, results in decreased variabilty and a larger spore. Drouth, in this particular case, seems to have induced a greater variability; and an uncongenial host reduced the spore size.

From all these results, it is evident that when all forms are grown under identical environmental conditions, a characteristic spore size does seem to predominate in any given physiologic form. The differences in size of spores between the various forms under such conditions, however, is less than the variation in the size of an individual form under varying environmental conditions. Consequently morphological differences, while they may serve still further to differentiate forms, can not be relied upon as an initial or sole means of identification.

OTHER DIFFERENCES BETWEEN THE FORMS

Forms 3 and 4 are very definitely characterized by the rapidity with which they form teliospores, as compared with the other forms. This is particularly marked with Form 4. In infections with Form 4, teliospores have been found to form within from 20 to 40 days following inoculation, depending on environmental conditions. With Form 3 the interval was usually but slightly longer; while it was very much longer with the other forms, when they formed teliospores at all. Under parallel conditions, teliospores consistently developed from 10 to 15 days earlier with Form 3 and 4 than with Forms 1 and 2. Since the teliospores also formed slightly sooner with Form 4 than with Form 3, there is the interesting suggestion that there is some correlation between the virulence of the form and the interval required to produce teliospores.

RELATION BETWEEN THE PATHOGENE AND THE HOST PLANT

The histological details of the infection of various wheat varieties by *Puccinia graminis* has been rather adequately worked out by

Stakman (28), Newton (23), Allen (1) and others. From their work it is evident that resistance in wheat varieties depends primarily on physiologic rather than on morphologic differences.[4] The delicate physiologic balance which determines resistance is specific against certain rust forms and is not necessarily maintained in the same way even toward very similar forms.

A parallel study of the infection of oats by *P. graminis avenae* seemed desirable. The problems presented in this connection, however, were so numerous that little more than a beginning could be made on them in an investigation of such wide scope as the present one.

The different types of hypersensitiveness, which are so varied, and in many respects different from those encountered in wheat stem rust infections, deserve special investigation.

The present work has been limited to a preliminary study of the infection on Victory as a type of thoroly susceptible host, and of Richland when attacked (1) by a form of rust to which it is susceptible and (2) by a form to which it is resistant.

The infection of a susceptible variety of oats, as typified by Victory, does not seem significantly different from the infection of a susceptible wheat variety. An appressorium forms over the stoma and from this a minute penetration tube passes through the stomatal opening. The contents of the appressorium flow through this tube and form a substomatal vesicle just under the stoma. From this substomatal vesicle, hyphae grow out in all directions among the adjoining cells. Haustoria are formed fairly abundantly, especially by the younger hyphae. Except where the infection is very heavy or where uredinia are being formed, there is very little killing of host tissue.

When Richland is infected by Form 4, to which it is completely susceptible, the process seems identical with that described for Victory. Illustrations of this type of infection are shown in Plate 7.

When Richland is inoculated with Form 2, to which it is markedly resistant, fewer germ tubes appear to enter the leaf than when it is inoculated with Form 4. This does not seem to be due to any mechanical difficulty in penetration, because a great many germ tubes do enter, and the penetration is quite normal. Indeed, in such cases the actual penetration tube may be small as compared with the stomatal opening. In many cases, however, the germ tubes wander aimlessly over the surface of the leaf or form appresoria which apparently never develop further. It seems rather that the rust fungus responds to some

[4] Since this manuscript was prepared, Hursh has published (42) the results of a cooperative investigation between the U. S. Department of Agriculture and the University of Minnesota in which he found that certain varieties of wheat are resistant to *P. graminis* on account of morphological peculiarities.

stimulus normally exerted by a congenial host and this stimulus is more or less specific to physiologic forms capable of infecting the particular host.

The hyphae that do enter behave very similarly to those described in the susceptible variety. The chief difference seems to be in the response of the host. Local killing is common and often very pronounced. The first indication of cell degeneration seems to be a slight plasmolysis. Then the chloroplasts and nucleus swell, the cell becomes very turgid, quickly disorganizes, and plasmolysis and complete degeneration follow. The process is gradual, however, and the fungus manages to produce small uredinia conspicuously lacking in vigor before its development is checked by the death of the host tissue. It is often surprising, tho, especially when environmental conditions are optimum and infection light, how far the development of the fungus may proceed before any indication of hypersensitiveness on the part of the host is evident. On the other hand, a marked hypersensitiveness rather frequently accompanies a very heavy infection on thoroly susceptible varieties like Victory. Much remains to be learned of the nature of resistance to oat rust and of the significance of hypersensitiveness in both resistant and susceptible varieties.

GRASS-HOST RANGE OF PHYSIOLOGIC FORMS

One of the most striking facts disclosed by a preliminary study of the epidemiology of oat stem rust in Western Canada is the apparent scarcity of grass hosts. *Dactylis glomerata* L., which is so commonly infected by *P. graminis avenae* wherever it occurs, has been introduced so sparingly in Western Canada that it is of slight importance in relation to oat rust.

During 1923 oat rust was collected only on *Avena sativa* L., *A. fatua* L., and *Hierochloe odorata* (L.) Wahlenb. A greenhouse investigation was undertaken to determine whether or not such a limited grass-host range represented the true condition in oat stem rust and whether the several physiologic forms differ markedly in their grass-host range.

About twenty species of grasses belonging to thirteen genera have been inoculated with the various physiologic forms. The results are presented in Table XVII. It will be noticed that the forms were very similar in their infection capabilities. The results may be summarized briefly as follows:

Hosts easily infected by artificial inoculation: *D. glomerata* L. and *Avena fatua* L.

Hosts weakly to moderately infected: *Agropyron caninum* (L.), Beauv.; *A. richardsonii* Schrad.; *Arrhenatherum elatius* (L.) Beauv.;

Bromus ciliatus L.; *Bromus purgans* L.; *Elymus curvatus* Piper; *Lolium perenne* L.; *Stipa viridula* Trin.

Hosts inoculated but not infected: *Andropogon scoparius* Mich.; *Agrostis verticillata* Vill.; *Agrostis retrofacta; Bromus inermis* Leyss.; *Elymus canadensis* L.; *Elymus virginicus* L.; *Hordeum jubatum* L.; and *Setaria glauca* (L.) Beauv.

Unfortunately, some of the more likely grass hosts were not available. Until these have been investigated, along with many others, it seems unwise to draw any sweeping conclusions. The results to date indicate, however, that the grass-host range of oat stem rust is rather limited.

It is extremely interesting to notice that the infection capabilities of the Swedish and South African forms parallel very closely those of our native forms. If physiologic forms arise through adaptation, as is sometimes postulated, the foreign forms might be expected to react differently from our native forms on our native grasses, but they did not.

In the light of the results obtained, it seems doubtful whether an extended investigation of the grass-host range of oat stem rust would be especially valuable. Thus, it will be noticed that one sample of *Dactylis glomerata* L. was uniformly resistant, while another sample was uniformly susceptible. That this variability in resistance is quite general in *Dactylis* was indicated by examination of this species in the grass plots at Manitoba Agricultural College. Moreover, it will be obvious from a study of Table XVII that this variability in resistance is not confined to *Dactylis glomerata.* Many cases are evident where a great variation in resistance occurred among the plants of a given species when infected by a single physiologic form. This variability is probably an expression of the heterozygosity of these, for the most part, open-pollinated plants. Therefore, it is unsafe to conclude that the resistance of a particular sample of grass worked with in the greenhouse represents the condition of that species as a whole. In general, the data secured by determining the form of rust present on naturally rusted grasses seem more significant and more desirable.

TABLE XVII

RESULTS OF INOCULATING GRASSES WITH *P. graminis avenae*, FORMS 1, 2, 3, 4, AND 5

Grass inoculated	Form 1		Form 2		Form 3		Form 4		Form 5	
	Results*	Character of infection	Results	Character of infection	Results	Character of infection	Results	Character of infection	Results	Character of infection
Agropyron caninum (L.) Beauv.	20 / 150;60	Weak	6 / 80;30	Weak	1 / 76;19	Weak; flecks sharply necrotic	15 / 128;32	Weak; flecks sharply necrotic	0 / 150;70	Flecks faint
Agropyron richardsonii Schrad.	0 / 80;60	Flecks sharply necrotic	35 / 40	Very weak	10 / 66;30	Very weak	5 / 80;46	Very weak	30 / 70;10	Very weak
Avena barbata Brot.	6 / 7	Vigorous	10 / 10	Vigorous	10 / 10	Vigorous	14 / 14	Vigorous	10 / 12	Vigorous
Andropogon scoparius Michx.	0 / 60;50	Flecks indistinct	0 / 114;110	Flecks minute; sharply necrotic	0 / 96;80	Flecks indistinct	0 / 82;68	Flecks indistinct	0 / 115;98	Flecks sharply necrotic
Andropogon furcatus Muhl.	0 / 50;42	Flecks indistinct	0 / 58;34	Flecks indistinct	0 / 69;42	Flecks indistinct	0 / 86;41	Flecks indistinct	0 / 75;50	Flecks indistinct
Agrostis verticillata Vill.	0 / 46;18	Flecks indistinct	0 / 62;12		0 / 50;0		0 / 57;0		0 / 66;0	
Agrostis retrofacta	0 / 24;0		0 / 32;0		0 / 40;0		0 / 27;0		0 / 43;0	
Arrhenatherum elatius (L.) Beauv.	8 / 42;14	Weak	26 / 38	Weak to moderate	13 / 51;20	Moderate to very weak	22 / 58	Moderate	27 / 46	Weak to moderate
Bromus inermis Leyss.	0 / 20;10	Flecks indistinct	0 / 20;20	Flecks discolored, sharply necrotic	0 / 28;7	Flecks indistinct	0 / 30;0		0 / 30;15	Flecks distinct; infection weak
Bromus ciliatus L.	40 / 60	Moderate	33 / 43;6	Weak to moderate	17 / 70;27	Moderate	18 / 40	Moderate	20 / 60;32	Flecks distinct; infection weak

TABLE XVII—*Continued*

Grass inoculated	Form 1 Results	Form 1 Character of infection	Form 2 Results	Form 2 Character of infection	Form 3 Results	Form 3 Character of infection	Form 4 Results	Form 4 Character of infection	Form 5 Results	Form 5 Character of infection
Bromus purgans L.	0/96;70	Flecks; discolored	96/105	Very weak; uredinia small; much hypersensitiveness	10/160;140	Very weak; much necrosis	0/150;138	Flecks necrotic and discolored	50/130;40	Weak
Dactylis glomerata L.	12/12	Weak	25/28	Weak	12/18	Weak	20/22	Weak	15/15	Weak
Dactylis glomerata L.	14/20	Vigorous	18/19	Vigorous	26/40	Vigorous	26/45	Vigorous	32/36	Vigorous
Elymus canadensis L.	0/70;52	Flecks minute and necrotic	1/88;86	Flecks minute, distinct, necrotic. One plant susceptible	0/92;92	Flecks faint to sharply necrotic	0/101;98	Flecks numerous; sharply necrotic	0/75;60	Flecks minute; sharply necrotic
Elymus curvatus Piper.	20/66;40	Weak; flecks faintly to sharply necrotic	44/134;20	Variable, weak to moderate; flecks indistinct	31/122;52	Weak; flecks faint to sharply necrotic; uredinia small	58/33;41	Variable; weak to moderate; flecks faint to sharply necrotic	0/80;61	Flecks distinct
Elymus virginicus L.	0/50;38	Flecks distinct	0/46;0		4/41;5	Weak; uredinia very small; hypersensitiveness very pronounced	0/20;5	Flecks indistinct	0/40;10	Flecks indistinct
Hordeum jubatum L.	0/14;0		0/24;0		0/18;0		0/32;0		0/28;0	
Lolium perenne L.	0/68;42	Flecks distinct	0/45;23	Flecks distinct	0/76;45	Flecks distinct	0/26;20	Flecks indistinct	0/31;15	Flecks indistinct
Setaria glauca (L.) Beauv.	0/60;0		0/50;6	Flecks indistinct	0/66;0		0/70;0		0/60;10	Flecks indistinct
Stipa viridula Trin.	0/50;38	Flecks distinct	0/55;48	Flecks sharply necrotic	80/98;16	Weak; uredinia small; hypersensitiveness present	0/83;70	Flecks sharply necrotic	0/60;60	Sharply necrotic

* Numerator=number of plants infected; denominator=total number inoculated. Figures following semicolon (;) indicate number of plants flecked.

FIELD TESTS OF OAT VARIETIES

The reaction of a large number of oat varieties to stem rust under field conditions was tested at Winnipeg and Brandon, Manitoba, and at Indian Head, Saskatchewan. It was hoped that additional differential hosts might thus be discovered. Also, since the varieties White Tartar and Richland were included in each test, the experiment served as an additional test of the occurrence of Forms 3 and 4.

At Winnipeg, one rod row of each of eighty-five varieties was grown. Twenty-five of these varieties were grown at Brandon and at Indian Head. In each case, varieties belonging to the six species of *Avena*—*A. nuda, A. brevis, A. strigosa, A. sterilis, A. sativa,* and *A. orientalis*—were included in the test. The varieties grown at the three places, together with the percentage of infection which developed in each case are included in Table XVIII.

TABLE XVIII
FIELD TESTS OF VARIETAL RESISTANCE OF OATS TO STEM RUST

Variety	Classification	Severity of infection (per cent)					
		Winnipeg, Man.		Brandon, Man.		Indian Head, Sask.	
		Main crop	Late growth	Main crop	Late growth	Main crop	Late growth
Avena nuda	*A. nuda*	60	..	60	..	5	60
Avena strigosa	*A. strigosa*	45	..	60-75	..	5	40
Avena brevis	*A. brevis*	50	..	75-80	..	20	50
Avena sterilis nigra	*A. sterilis*	50	80	..	..	5	50
Avena sterilis (selection)	do	65	80	80-90	..	90	..
Red Rustproof	do	80	95	90-95	..	85	..
Burt	do	35	90	10	90	10	90
King	do	50-90	95	85-95	..	95	..
Okl. 606	do	80	95	80-95	..	10	75
Winterturf	*A. sativa*	90	..	..	..	..	..
Culbertson	do	85	..	..	..	..	..
Black Norway	do	75	90	..	..	..	..
Victor	do	45	90	..	..	..	..
Monarch, C.I. 1876	do	35	95	40	90	5	75
Black Mesdag, C.I. 1877	do	30	90	..	..	tr	..
Black Diamond	do	40	95	..	..	..	..
Monarch Diamond	do	50	95	..	..	..	..
Variety 703	do	30-80	..	..	..	..	..
Joanette, Minn. 550	do	40	95	50	90	..	..
C.I. 620	do	45	95	..	..	..	..
Danish Island	do	30	95	..	..	..	..
Early Gothland, C.I. 1723	do	15	95	..	..	..	..
Belyak, C.I. 1630	do	15	95	..	..	..	..
Silvermine, Minn. 506	do	20	90	..	..	..	..
Scottish Chief	do	10	85	..	..	..	..
June	do	50	95	..	..	..	..
Swedish Select, C.I. 802	do	20	95	..	..	..	..
Lincoln, C.I. 1463	do	40	90	..	..	..	..
Garton 748	*A. orientalis*	25	95	20	95	tr	70
Garton 784	do	20	90	10-15	90	15	80
Garton Grey	do	50	95	40	95	20	85
Black Tartarian	do	50	95	80	95	20	60
Golden Giant, C.I. 1606	do	45	70	70	95	10	70
Sparrowbill, C.I. 1604	do	55	90	80	95	30	65

TABLE XVIII—*Continued*

Variety	Classification	Severity of infection (per cent)					
		Winnipeg, Man.		Brandon, Man.		Indian Head, Sask.	
		Main crop	Late growth	Main crop	Late growth	Main crop	Late growth
Garton 585	*A. orientalis*	60	90	..	..	..	..
Tartar King	do	5	95	60	95	10	65
Storm King, C.I. 1602	do	15	90	80	90	5	75
White Tartar	do	5	5	..	..	..	..
Green Mountain	do	3	3	..	..	..	..
White Tartar, C.I. 1614	do	3	3	..	..	..	..
North Finnish, C.I. 1882	*A. sativa*	50	95	..	..	5	60
Gar. 473	do	50	95	..	..	..	..
Gar. 691	do	75	95	..	..	..	..
Kherson	do	50	98	tr	90	tr	..
Kherson selection	do	55	98	5	95	tr	..
60-Day, C.I. 826	do	55	98	10	90	tr	..
60-Day selection	do	5	90	5	90	..	..
Early Champion, C.I. 1623	do	tr	95	..	..	..	..
Awnless Probsteier	do	30	95	..	..	..	..
Japan selection	do	40	95	..	..	..	..
Golden Drop	do	10	95	..	..	..	..
C.I. 603	do	35	95	..	..	..	..
Green Russian, Iowa 96	do	40	95	..	..	..	..
Canadian, C.I. 1625	do	35	95	..	..	..	..
Tobolsk, C.I. 1709	do	50	95	..	..	..	..
Silvermine selection	do	55	95	..	..	..	..
C.I. 602	do	40	95	..	..	..	..
Early Dakota	do	35	95	..	..	..	..
Irish Victor, C.I. 1896	do	20	95	..	..	..	..
White Tartar, Minn. 539	do	3	3	tr	tr	tr	20(2)
Albion, C.I. 729	do	10	95	..	..	..	..
Early Mt., C.I. 1624	do	80	..	..	..	..	..
Standwell, C.I. 1975	do	75	80	..	..	..	..
Empire, C.I. 1974	do	50	90	..	..	..	..
Old Island Black, C.I. 1881	do	65	95	..	..	..	..
Idamine, C.I. 1834	do	65	90	..	..	..	..
Black American, C.I. 1758	do	50	95	..	..	..	..
Wisconsin No. 7, C.I. 1154	do	40	90	..	..	..	..
Iowar, C.I. 847	do	30	90	..	..	..	..
Richland, Iowa 105	do	3	3	tr	tr	tr	tr
Nebraskas, No. 21. C.I. 841	do	10	90	..	..	..	..
Cornwall, C.I. 1317	do	65	95	..	..	..	..
Kanata, C.I. 839	do	75	95	..	..	..	..
Ferguson Navarra, C.I. 966	do	60	90	..	..	..	..
C.I. 749	do	35	80	..	..	..	..
C.I. 836	do	30	75	..	..	..	..
Red Rustproof, C.I. 1356	*A. sterilis*	90	95	..	..	..	..
Golden Rain, C.I. 1718	*A. sativa*	35	90	..	..	..	..
Cole, C.I. 843	do	3	90	..	..	..	..
Cornellian, C.I. 1843	do	10	95	..	..	..	..
Richland, C.I. 787	do	3	3	..	..	..	..
Aurora	do	90	..	..	..	..	..
Red Texan	do	90	..	..	..	..	..
Richland, K.S. 209	do	5	3	..	..	..	..
Banner	do	40	95	90	85	..	..

From a study of this table it is evident that, while some varieties matured early enough to escape heavy infection, few possessed any resistance. Indeed, resistance seemed entirely lacking except where it was already known to be present, i.e., in the differential varieties White Tartar, Richland, and Strain 703. In Strain 703, occasional plants were found quite evidently infected by Form 1 as well as by a form to which they were susceptible. In such cases, the weaker form was very largely obscured.

The fact that White Tartar and Richland were consistently resistant at all three places is extremely interesting. It is to be hoped that further investigation will support this indication of the absence in America of Forms 3 and 4, which are so virulent. The resistance of these varieties in the field tests, together with the fact that they were resistant to all native collections of oat rust from either the United States or Canada, is certainly an indication that Forms 3 and 4 are rare if they occur at all in this country. Since a limited distribution is difficult to reconcile with the virulence and extended host range of these forms, it seems more probable that they do not occur at all in America. If this can be established with reasonable certainty, it will simplify the problem to the extent at least that varieties with resistance adequate to withstand all our indigenous forms will be available.

GEOGRAPHICAL DISTRIBUTION

The sources of 65 collections made during 1921, 1922, and 1923 are given in Table XIX. For the sake of completeness, 23 forms already reported on by Stakman, Levine, and Bailey, (33) are included.

Form 1 is common in occurrence and is widely distributed. It has been collected from Saskatchewan to Mexico.

Form 2 seems even more abundantly distributed than Form 1 in the central and northern parts of North America, extending to about 500 miles north of Winnipeg, in Maine and Mexico, as well as in South Africa and Sweden.

Forms 3 and 4 have not been found in North America. In view of the number of collections made and the very wide territory covered by them, it seems that these forms must be very limited in distribution, if they occur at all in this region.

Form 5, while of somewhat less frequent occurrence than Forms 1 and 2, seems also widespread.

TABLE XIX

DISTRIBUTION OF PHYSIOLOGIC FORMS OF STEM RUST OF OATS

Physiologic form	Place of collection	Collector	Original host
P. graminis avenae, Form 1	Zelma, Sask.	W. P. Fraser	*Avena sativa*
	Litchfield, Minn.	L. W. Melander	do
	Rosetown, Minn.	M. N. Levine	do
	Lafayette, Ind.	W. Butler	do
	St. Paul, Minn.	F. Griffee	do
	Boerne, Tex.	W. Butler	do
	San Antonio, Tex.	W. Butler	do
	Robards, Tex.	W. Butler	do
	Huntley, Ill.	J. L. Seal	do
	Cartwright, Man.	I. L. Conners	do
	Carlyle, Sask.	P. M. Simmonds	do
	Dauphin, Man.	D. L. Bailey	do
	Piedras Negras, Mex.	E. C. Stakman	do
	Neepawa, Man.	R. C. Russell	do
P. graminis avenae, Form 2	Saskatoon, Sask.	W. P. Fraser	do
	Zelma, Sask.	W. P. Fraser	do
	Presque Isle, Me.	F. Weiss	do
	Litchfield, Minn.	L. W. Melander	do
	Rosetown, Minn.	M. N. Levine	do
	Redfield, S. D.	M. N. Levine	do
	Huron, S. D.	M. Lapidus	do
	Lafayette, Ind.	W. Butler	do
	Chillicothe, Mo.	W. Butler	do
	Norman, Okla.	W. Butler	*Dactylis glomerata*
	Lawton, Okla.	H. Ostrom	*Avena sativa*
	San Marcos, Tex.	W. Butler	do
	Robards, Tex.	W. Butler	do
	Saltillo, Mex.	E. C. Stakman	do
	Potchefstroom, S. Africa	G. F. Puttick	do
	Brockway, Mich.	E. B. Lambert	do
	Berens River, Man.	G. R. Bisby	do
	Carman, Man.	R. C. Russell	do
	Dauphin, Man.	F. J. Greaney	do
	Dauphin, Man.	D. L. Bailey	*Avena fatua*
	Carlyle, Sask.	P. M. Simmonds	*Avena sativa*
	Edmonton, Alta.	W. P. Fraser	do
	Grandview, Man.	R. C. Russell	do
	Hendrum, Minn.	J. J. Christensen	do
	Letellier, Man.	D. L. Bailey	*Avena fatua*
	Lashburn, Sask.	W. P. Fraser	*Avena sativa*
	Morris, Man.	D. L. Bailey	do
	Melfort, Sask.	W. P. Fraser	do
	Litchfield, Minn.	L. W. Melander	do
	Moose Jaw, Sask.	W. P. Fraser	do
	Norway House, Man.	G. R. Bisby	do
	Neepawa, Man.	R. C. Russell	do
	Roblin, Man.	R. C. Russell	do
	Saltcoats, Sask.	W. P. Fraser	do
	Stonewall, Man.	R. C. Russell	do
	Indian Head, Sask.	D. L. Bailey	do
	Neepawa, Man.	R. C. Russell	do
	Morris, Man.	D. L. Bailey	*Avena fatua*
P. graminis avenae, Form 3	Upsala, Sweden	E. C. Stakman	*Avena sativa*
	Potchefstroom, S. Africa	G. F. Puttick	do
P. graminis avenae, Form 4	Upsala, Sweden	E. C. Stakman	do

TABLE XIX—*Continued*

Physiologic form	Place of collection	Collector	Original host
P. graminis avenae,	Zelma, Sask.	W. P. Fraser	*Avena sativa*
Form 5	Rosthern, Sask.	W. P. Fraser	*Torresia odorata*
	Swan River, Man.	D. L. Bailey	*Avena sativa*
	St. Jean, Man.	D. L. Bailey	*Avena fatua*
	Roblin, Man.	R. C. Russell	*Avena sativa*
	Minnetonas, Man.	F. J. Greaney	do
	Morden, Man.	R. C. Russell	do
	Erickson, Man.	F. J. Greaney	do
	Gretna, Man.	D. L. Bailey	*Avena fatua*
	Brandon, Man.	I. L. Conners	*Avena sativa*
	Assiniboia, Sask.	W. P. Fraser	do
	Carman, Man.	R. C. Russell	do
	Snake Island, Man.	G. R. Bisby	do
	Swift Current, Sask.	W. P. Fraser	do
	Carlyle, Sask.	P. M. Simmonds	do

DISCUSSION AND CONCLUSION

The comparatively slight degree of specialization which appears to exist in *P. graminis avenae* will be striking to any one familiar with the marked degree of specialization which has been shown to exist in *P. graminis tritici* (32). Why this apparently slight degree of specialization should be the case is an interesting subject for speculation. The fact that five physiologic forms have been distinguished suggests that there may be still more. This idea is further supported by the rather marked variability in the reaction of White Tartar and perhaps also by the heterogeneous infection on the Joanette Strain. Moreover, a fairly close approximation of the total number of physiologic forms which could be isolated with the number of differential hosts available has been reached. This is more evident when it is remembered that Joanette Strain and Strain 703 react virtually identically and that Monarch Strain, Richland, and Heigira Strain also react as a single group with apparently identical resistance. If a degree of specialization approximating that of *P. graminis tritici* be assumed, some difference must exist in the origin or nature of oat varieties as compared with wheat varieties. Only in this way could the lack of differential hosts necessary to isolate more physiologic forms of oat rust be explained. Such a difference is not immediately apparent. A comparison of the chromosome number in wheat and oat species is interesting. In wheat we have the haploid numbers 7, 14, and 21 in the Einkorn, Emmer, and Spelt groups, respectively. In oats (27), the species *Avena brevis, A. barbata,* and *A. strigosa* have 7 or 14 chromosomes as compared with 21 for *A. sativa.* From this it is evident that an equal range in chromosome number provides an equal chance for as great variability in oat varieties as in wheat. If such a variability is lacking in oat varieties, therefore, the only explanation presenting itself, in addition to the recognized fact that natural crossing occurs more rarely in oats, seems to be that mutations are also rare in oats as compared with wheat.

From a practical standpoint, these investigations give us still further cause for believing that the resistance of such varieties as White Tartar and Richland will be adequate to withstand the attack of all our native physiologic forms. If such be the case, the oat stem rust problem may be regarded as well on the way to solution, through the work of Parker (24, 25), Garber (10), Griffee (11), and others. As a safeguard against the occurrence or possible introduction of such virulent forms as 3 and 4, the search for a variety uniformly resistant to all the physiologic forms of *P. graminis avenae* should be continued.

SUMMARY

1. Five physiologic forms of *Puccinia graminis avenae* have been distinguished, and the characteristic reaction of each on several differential hosts is described.

2. In addition to differences in parasitism, significant differences in the size of the urediniospores were found between some of the physiologic forms when all were grown under identical conditions. In such cases, however, the differences were less than the fluctuations induced in a single form by varying the environmental conditions. Therefore morphologic differences alone could not be relied upon as a means of identifying the individual forms.

3. A preliminary study of the grass-host range of the five physiologic forms is reported on. The infection capabilities of the five forms are remarkably similar and the host range seems to be decidedly limited.

4. The geographic distribution of 14 cultures of Form 1, 38 cultures of Form 2, 15 cultures of Form 5, two cultures of Form 3, and one of Form 4 is given. Form 4 is of Swedish origin and has not been found in North America. Two cultures of Form 3, one from Sweden and one from South Africa, have been studied, but none of American origin has been found. Forms 1, 2, and 5 are very widely distributed throughout the United States and Canada.

5. Field tests of a large number of oat varieties were made at Indian Head, Saskatchewan, and at Brandon and Winnipeg, Manitoba. The uniform susceptibility of all the varieties except White Tartar and Richland, indicated the possible presence in these localities of Forms 1, 2, and 5 and the definite absence of Forms 3 and 4.

6. The infection of Victory, which is susceptible to all five physiologic forms, proceeds in a manner similar to that of wheat varieties susceptible to *P. graminis tritici.* Penetration is stomatal, an appressorium forms over the stoma, a very small penetration tube passes through the stomatal opening, and the contents of the appressorium

flow through and form a substomatal vesicle beneath. There is very little killing of host tissue except where uredinia are formed.

7. The resistance of Richland seems not at all dependent on morphologic characters. The mode of infection is much the same as in a susceptible variety except that pronounced local killing of the infected tissue seems to limit the development of the fungus.

LITERATURE CITED

1. Allen, Ruth F. A cytological study of infection of Baart and Kanred wheats by *Puccinia graminis tritici.* Jour. Agr. Res. 23:131-151. 1923.
2. Carleton, M. A. Cereal rusts of the United States. U. S. Dept. Agr., Div. Veg. Physiol. and Path. Bul. 16. 1899.
3. ————. Investigation of rusts. U. S. Dept. Agr., B.P.I. Bul. 63. 1904.
4. Eriksson, Jacob. Über die Specialisirung des Parasitismus bei den Getreiderostpilzen. Ber. Deutsch. Bot. Gesell. 12:292-331. 1894.
5. Ist die verschiedene Widerstandfahigkeit der Weizensorten gegen Rost konstant oder nicht? Zeit. Pflanzenk. 5:198-200. 1895.
6. ———— and Henning, Ernst. Die Getreideroste, VII. 464 p. Stockholm. 1896.
7. Fraser, W. P. Strains of stem rust in wheat; preliminary report. Dom. Can. Dept. of Agr., Div. Botany Interim Report for year ending March 31, 1922, pp. 64-65. 1922.
8. ———— and Bailey, D. L. Biologic forms of wheat stem rust in western Canada. Phytopath. 11:202. 1921.
9. Freeman, E. M. and Johnson, E. C. The rusts of grains in the United States. U. S. Dept. Agr., B.P.I. Bul 216. 1911.
10. Garber, R. J. Inheritance and yield with particular reference to rust resistance and panicle type of oats. Minn. Agr. Exp. Sta. Tech. Bul. 7, pp. 1-62. 1922.
11. Griffee, Fred. Breeding oats resistant to stem rust. Jour. Hered. 13:187-190, 3 fig. 1922.
12. Hitchcock, A. S. and Carleton, M. A. Second report on rust of grain. Kan. Agr. Exp. Sta. Bul. 46. 1894.
13. Hoerner, G. R. Biologic forms of *Puccinia coronata* on oats. Phytopath. 9:309-314. 1919.
14. ————. Infection capabilities of crown rust of oats. Phytopath. 12:4-15. 1922.
15. Hungerford, Charles W. and Owens, C. K. Specialized varieties of *Puccinia glumarum* and hosts for variety *tritici.* Jour. Agr. Res. 25:363-401. 1923.
16. Jaczewski, A. von. Studien über das Verhalten das Schwarzrostes des Getreides in Russland. Zeit. Pflanzenk. 20:321-359. 1910.
17. Johnson, E. C. Timothy rust in the United States. U. S. Dept. Agr., B.P.I. Bul. 224, pp. 1-22. 1911.
18. Leach, Julian G. The parasitism of *Puccinia graminis tritici* Erikss. and Henn. and *P. graminis tritici-compacti,* Stak. and Piem. Phytopath. 9: 59-88. 1919.
19. Levine, M. N. A statistical study of the comparative morphology of biologic forms of *Puccinia graminis.* Jour. Agr. Res. 24:539-567. 1923.
20. ———— and Stakman, E. C. A third biologic form of *Puccinia graminis* on wheat. Jour. Agr. Res. 13:651-654. 1918.

21. ————. Biologic specialization of *Puccinia graminis secalis*. Phytopath. 13:35. 1923.
22. Mains, E. B. and Jackson, H. S. Two strains of *Puccinia triticina* on wheat in the United States. Phytopath. 11:40. 1921.
23. Newton, Margaret. Studies in wheat stem rust (*Puccinia graminis tritici*). Trans. Royal Soc. Can. 3rd series. 16:153-210. 1922.
24. Parker, John H. Greenhouse experiments on the rust resistance of oat varieties. U. S. Dept. Agr. Bul. 629, pp. 1-16. 1918.
25. ————. A preliminary study of the inheritance of rust resistance in oats. Jour. Amer. Soc. Agron. 12:23-38. 1920.
26. Reed, George M. Physiological specialization of parasitic fungi. Brooklyn Botanic Garden Memoirs 1:348-409. 1918.
27. Sax, Karl. The relation between chromosome number, morphological characters, and rust resistance in segregates of partially sterile wheat hybrids. Genetics 8:301-321. 1923.
28. Stakman, E. C. A study in cereal rusts: Physiological races. Minn. Agr. Exp. Sta. Bul. 138. 1914. (Out of print.)
29. ————. Relation between *Puccinia graminis* and plants highly resistant to its attack. Jour. Agr. Res. 4:193-200. 1915.
30. ———— and Hoerner, G. R. The occurrence of *Puccinia graminis tritici-compacti* in the southern United States. Phytopath. 8:141-149. 1918.
31. ———— and Levine, M. N. Effect of certain ecological factors on the morphology of the urediniospores of *Puccinia graminis*. Jour. Agr. Res. 16:43-77. 1919.
32. ————. The determination of biologic forms of *Puccinia graminis* on *Triticum spp.* Univ. of Minn. Agr. Exp. Sta. Tech. Bul. 8, pp. 1-10. 1922.
33. ———— and Bailey, D. L. Biologic forms of *Puccinia graminis* on varieties of *Avena spp.* Jour. Agr. Res. 24:1013-1018. 1923.
34. ———— and Leach, J. G. New biologic forms of *Puccinia graminis*. Jour. Agr. Res. 16:103-105. 1919.
35. ————, Parker, John H., and Piemeisel, F. J. Can biologic forms of stem rust of wheat change rapidly enough to interfere with breeding for rust resistance? Jour. Agr. Res. 14:111-123. 1918.
36. ———— and Piemeisel, F. J. A new strain of *Puccinia graminis*. Phytopath. 1:73. 1917.
37. ————. Biologic forms of *Puccinia graminis* on cereals and grasses. Jour. Agr. Res. 10:429-495. 1917.
38. ———— and Levine, M. N. Plasticity of biologic forms of *Puccinia graminis*. Jour. Agr. Res. 15:221-250. 1918.
39. Vavilov, N. I. Materially k voprosu ob ustoychivosti khlevnykh zlakov protiv parasiticheskikh grybov. Trudy Selec. Sta. Moscow, Agr. Inst. 1: 1-110. 1913.
40. Ward, H. M. The bromes and their rust fungus, *Puccinia dispersa* Erikss. Ann. Bot. 15:560. 1901.
41. ————. On the relations between host and parasite in the bromes and their brown rust, *Puccinia dispersa* Erikss. Ann. Bot. 16:233-315. 1902.
42. Hursh, C. R. Morphological and physiological studies on the resistance of wheat to *Puccinia graminis tritici* Erikss. and Henn. Jour. Agr. Res. 27: 381-411. 1924.

EXPLANATION OF PLATES

Plate 1.

Classes of host reaction: Resistant (R), susceptible (S), and indeterminate (I), as indicated by different types of infection (0, 1, 2, 3, 4, and X) produced by physiologic forms of *Puccinia graminis avenae* on different varieties of oats.

Class R. (Resistant), including 3 subclasses corresponding to infection types 0, 1, and 2.

a. Practically immune (Infection type 0). No uredinia are developed, but sharply defined hypersensitive flecks are usually present.

b. Extremely resistant (Infection type 1). Infection very light; uredinia minute and scattered and surrounded by very sharply defined necrotic areas.

c. Moderately resistant (Infection type 2). Infection light; uredinia usually small and scattered; hypersensitive areas varying from sharply defined necrosis to pronounced chlorosis.

Class S (Susceptible), including two subclasses, corresponding to infection types 3 and 4.

d. Moderately susceptible (Infection type 3). Infection moderate; uredinia midsized with a tendency to coalesce; true hypersensitiveness absent, but light chlorotic areas usually present.

e. Completely susceptible (Infection type 4). Infection normal and heavy; uredinia large, numerous, and confluent; hypersensitiveness entirely absent, but chlorosis may be present when cultural conditions are unfavorable.

Class I (Indeterminate), representing the heterogeneous (X) type of infection.

f. Heterogeneous reaction (Infection type X). Uredinia very variable, apparently including all types and quantities of infection, often on the same blade; no mechanical separation seems to be possible as, on reinoculation, spores from small uredinia may produce large ones, and vice versa. In general, the infection is ill-defined.

Plate 2.

Puccinia graminis avenae (Form 1). Two leaves each of (1) Joanette Strain, (2) Monarch Strain, (3) Strain 703, (4) White Tartar, (5) Richland, (6) Heigira Strain, and (7) Victory.

Plate 3.

Puccinia graminis avenae (Form 2). Two leaves each of (1) Joanette Strain, (2) Monarch Strain, (3) Strain 703, (4) White Tartar, (5) Richland, (6) Heigira Strain, and (7) Victory.

Plate 4.

Puccinia graminis avenae (Form 3). Two leaves each of (1) Joanette Strain, (2) Monarch Strain, (3) Strain 703, (4) White Tartar, (5) Richland, (6) Heigira Strain, and (7) Victory.

Plate 5.

Puccinia graminis avenae (Form 4). Two leaves each of (1) Joanette Strain, (2) Monarch Strain, (3) Strain 703, (4) White Tartar, (5) Richland, (6) Heigira Strain, and (7) Victory.

Plate 6.

Puccinia graminis avenae (Form 5). Two leaves each of (1) Joanette Strain, (2) Monarch Strain, (3) Strain 703, (4) White Tartar, (5) Richland, (6) Heigira Strain, and (7) Victory.

Plate 7.

A. Appressorium developed on Richland from an inoculation with *Puccinia graminis avenae,* Form 2.

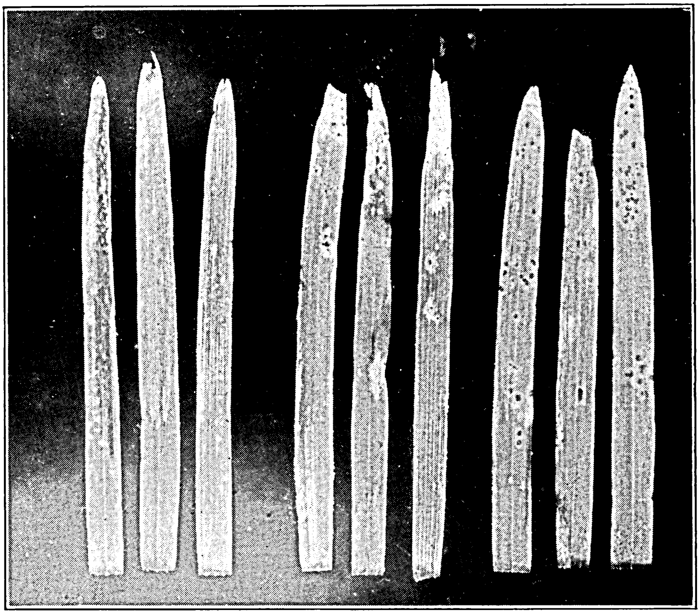
B. Entrance of penetration tube in Richland inoculated with Form 2.

C. Inner view of a stoma of Victory, 102 hours after inoculation with urediniospores of Form 2. Hyphae developed from substomatal vesicle.

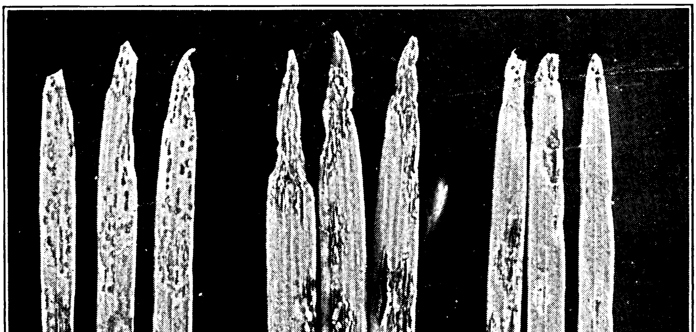
D. Cross-section of Richland showing method of entrance of Form 4.

E. Appressoria developing over stomata on Victory inoculated with Form 2.

PLATE I

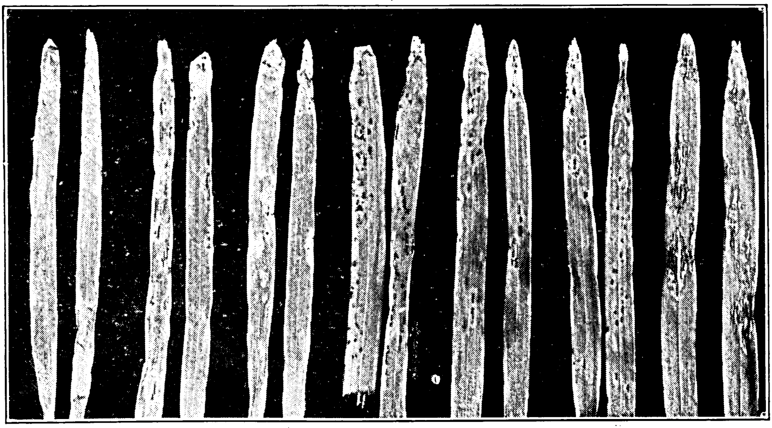


a b c



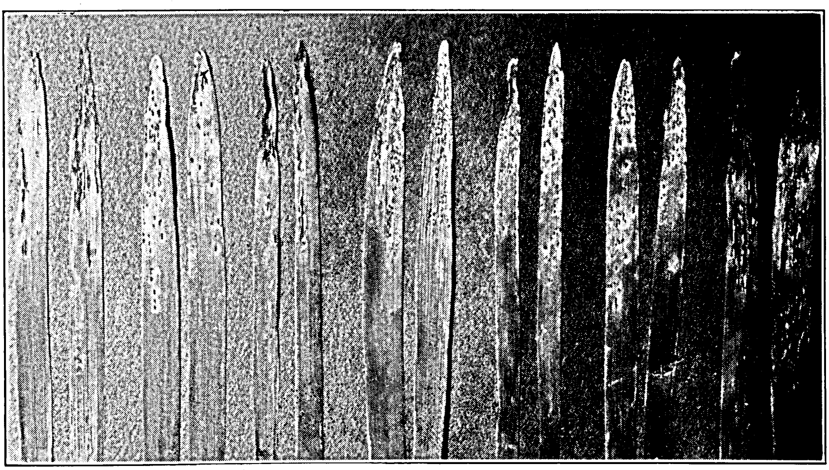
d e f

PLATE 2



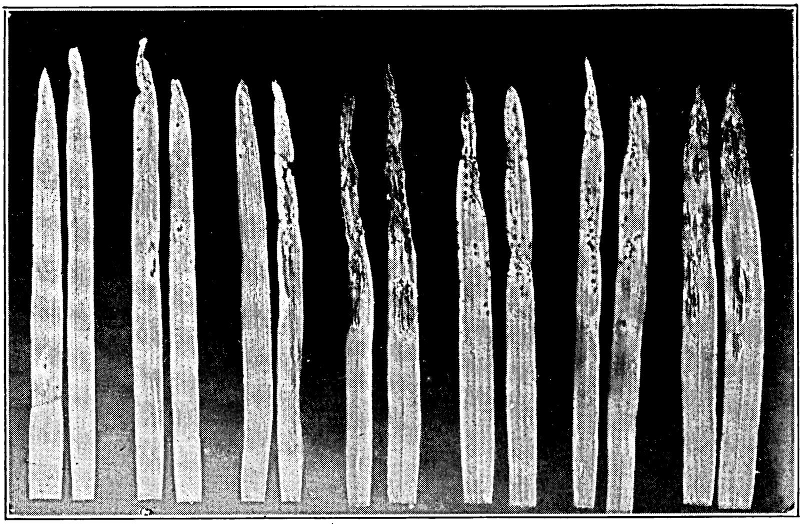
1 2 3 4 5 6 7

PLATE 3



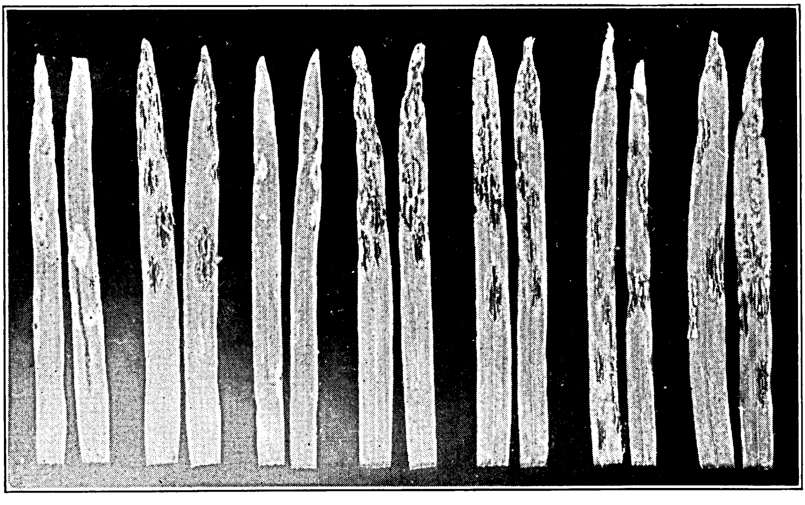
1 2 3 4 5 6 7

PLATE 4



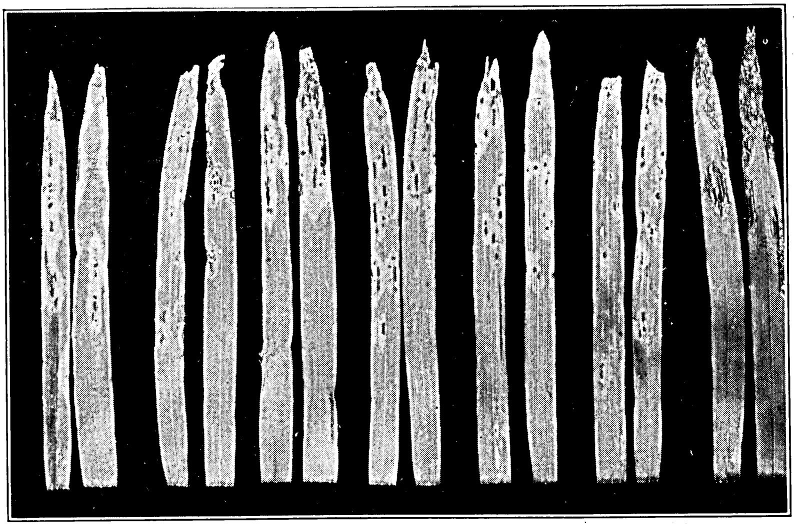
1 2 3 4 5 6 7

PLATE 5



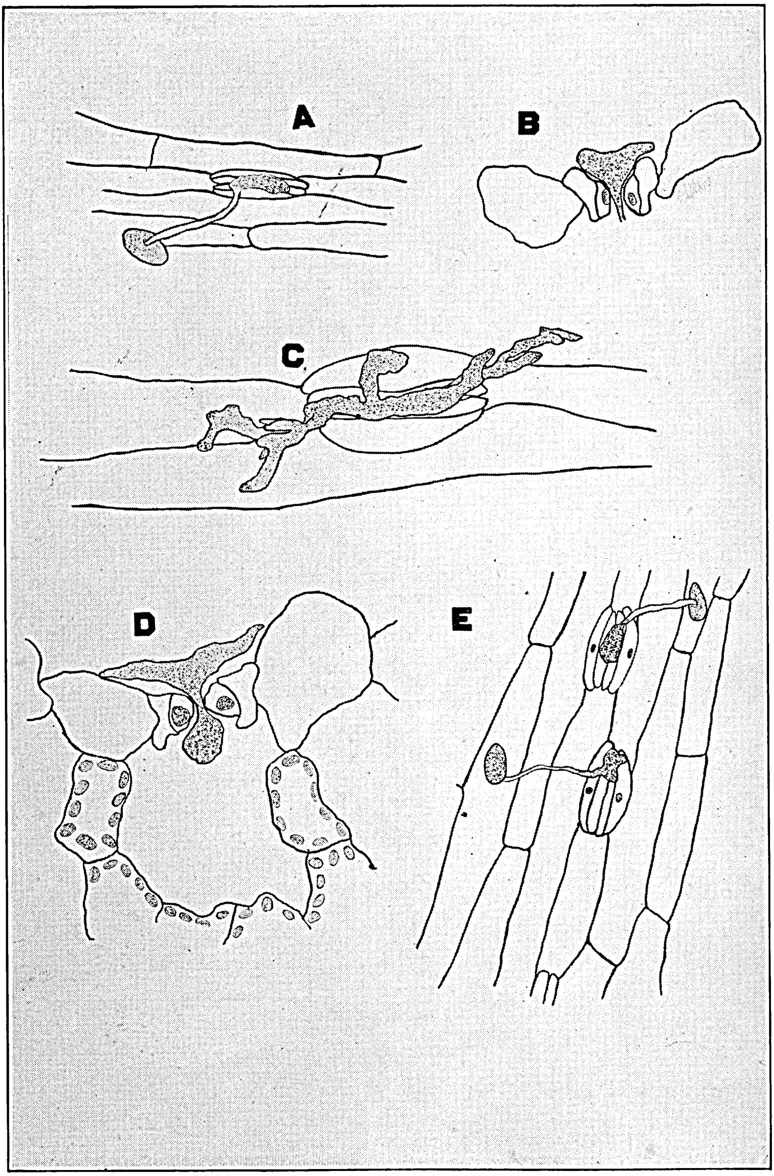
1 2 3 4 5 6 7

PLATE 6



1 2 3 4 5 6 7

PLATE 7



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